What the egg can tell about its hen: embryo development on the basis of Dynamic Energy Budgets.

Kooijman, S.A.L.M.

published in
Journal of Mathematical Biology
2009

DOI (link to publisher)
10.1007/s00285-008-0195-x

document version
Publisher's PDF, also known as Version of record

J. Math. Biol. (2009) 58:377–394
DOI 10.1007/s00285-008-0195-x

Mathematical Biology

What the egg can tell about its hen: Embryonic development on the basis of dynamic energy budgets

S. A. L. M. Kooijman

Received: 14 January 2008 / Revised: 17 April 2008 / Published online: 7 June 2008

Abstract The energy cost of offspring is important in the conversion of resources allocated to reproduction to numbers of offspring, and in obtaining energy budget parameters from quantities that are easy to measure. An efficient numerical procedure is presented to obtain this cost for eggs and foetusses in the context of the dynamic energy budget theory, which specifies that birth occurs when maturity exceeds a threshold value and maternal effects determine the reserve density at birth. This paper extends previous work to arbitrary values of the ratio of the maturity and somatic maintenance costs. I discuss the body size scaling implications for the relative size and age at birth and conclude that the size at birth, contrary to the age at birth, covaries with the maintenance ratio. Apart from evolutionary adaptation of the maturity at birth, this covariation might explain some of the observed scatter in the relative length at birth. The theory can be used to evaluate the effects of the separation of cells in e.g. the two-cell stage of embryonic development, and of the removal of initial egg mass. If cell separation hardly affects energy parameters, body size scaling relationships imply that cell separation can only occur successfully in species with sufficiently large maximum body length (as adult); i.e. some two times that of *Daphnia magna*. Toxic compounds that increase the cost of synthesis of structure, decrease the allocation to reproduction indirectly via the life cycle, because food uptake is linked to size. They can also decrease the egg size, however, such that the reproduction rate is stimulated at low concentrations. The present theory offers a possible explanation for this well-known phenomenon.

S. A. L. M. Kooijman (✉)
Department of Theoretical Biology, Vrije Universiteit, de Boelelaan 1087,
1081 HV Amsterdam, The Netherlands
e-mail: bas@bio.vu.nl

Keywords Dynamic energy budget theory · Embryonic development · Cost of an egg · Foetus · Incubation time · Length at birth · Body size scaling relationships · Removal of reserve · Hormesis

Mathematics Subject Classification (2000) 34B16 · 37N25

1 Introduction

The embryonic stage is rarely a topic of ecological texts, but nonetheless very important for the estimation of energy budget parameters [23]. Knowledge of energy costs of an embryo is required in the specification of the reproduction rates in models that deal with resource allocation. Knowledge of reproduction rates is basic for e.g. population dynamics and ecotoxicology, where effects of chemical compounds on reproduction rates are studied. The dynamics of the state variables of an embryo can also yield valuable information about the physiology of post-embryonic stages.

Twenty years ago I wrote a paper with the title "What the hen can tell about her egg" [18] demonstrating that the standard dynamic energy budget (DEB) model [19] captures egg development data very well for a number of species [19, Fig. 3.15–16], on the assumption that embryos behave as juveniles that do not eat and start their development with a negligibly small amount of structure. The model is meant to apply to all embryonic stages, such as eggs in animals, seeds in plants, spores in fungi and bacteria, as well as the pupation stage of holometabolic insects [19, Fig. 7.24].

The reserve density, i.e. the ratio of the amounts of reserve and structure, at birth tends to covary with that of the mother at egg production; well-fed mothers give birth to well-fed offspring. Such maternal effects are typical and have been found in e.g. birds [29], reptiles, amphibians [25], fishes [12], insects [26,31,32], crustaceans [9], rotifers [36], echinoderms and bivalves [3]. However, some species seem to produce large eggs under poor feeding conditions, e.g. some poeciliid fishes [30], daphnids [10] and *Sancassania* mites [2]. Moreover, egg size can vary within a clutch [6,28,35], according to geographical distribution [33], with age [26] and race.

DEB theory specifies the costs for structure, the somatic and maturity maintenance costs and the processes of growth and maturation. The additional specification of the reserve density at birth to accomodate maternal effects also specifies the initial amount of reserve (so the cost of an egg) indirectly, but its evaluation is not very simple. Maternal effects make that the cost per egg varies in time, with the consequence that this cost has to be evaluated for each time increment if reproduction rates are required as functions of time. This motives searching for an efficient algorithm.

Since [18] a lot of work has been done on many aspects of DEB theory, including work on the embryonic stage. (The next section summarizes the relevant aspects of the model.) The spectacular matches of model predictions with a much wider set of empirical data on embryonic growth and respiration on a wide variety of species [19,37,38] confirmed the existence of generally applicable rules for egg development as provided by DEB theory and motivated further work. It became clear that if the maturity and somatic maintenance rate coefficients are equal, stage transitions not only occur at exceeding threshold values for maturity, but also for structural mass (independent of the trajectory of food levels). If so, this simplifies matters considerably,

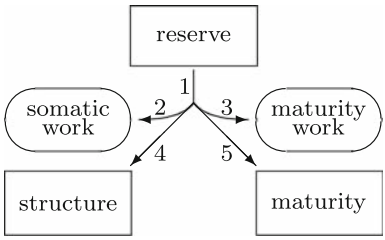

Fig. 1 The scheme of pools and fluxes as specified by the standard DEB model for egg development. The fluxes are, *1* mobilisation, *2* somatic maintenance, *3* maturity maintenance, *4* growth, *5* maturation

and the cost of an embryo can be obtained explicitly. It has been the reason to assume this equality in an early stage of the development of the DEB theory.

Over the years it became evident, however, that there is little theoretical ground for this equality and that size at birth (the initiation of assimilation) and puberty (the initiation of reproduction) do vary somewhat in response to variations in food availability (although much less than age at birth). This variation can be used to access the maturity maintenance rate coefficient [23]. Defence systems, such as the immune system, are fuelled from maturity maintenance, and parasites can affect it (see e.g. [8]) and so change the maturity maintenance rate coefficient. Toxicants can affect the somatic maintenance rate coefficient [14]. The implication is that size at birth and puberty must depend on the concentration of toxicant as well as on food density. This is exactly what has been observed [1]. These arguments prompted us to deal with the less simple case of unequal maintenance rate coefficients.

The primary aim of this paper is to present an efficient procedure to obtain the cost of an egg in the general case of unequal maturity and somatic maintenance rate coefficients. Moreover, I will discuss how the body size scaling relationships of DEB theory work out for this cost, and for the age and length at birth. Finally I discuss the results of egg size manipulations on the age and length at birth in the light of the standard DEB model. I start with the specification the standard model for embryonic development in the next section.

2 The standard DEB model for embryonic development

The standard DEB model for egg development can be summarised as follows: biomass consists of reserve and structure; the structure develops at the expense of the reserve, see Fig. 1. Structure requires (somatic) maintenance, reserve does not. Age zero is taken to coincide with the start of the growth of structure; the initial amount of structure is negligibly small. The mobilisation rate of reserve follows from weak and strong homeostasis assumptions [34]; a mechanism is presented in [24]. Allocation to growth and somatic maintenance (so to the soma) comprises a fixed fraction of mobilised reserve, the remaining fraction is allocated to maturation and maturity maintenance. The reserve density at birth equals that of the mother at embryo production. The transition to the juvenile stage (i.e. birth) occurs by initiating assimilation when the maturity exceeds a threshold value.

Foetal development represents a variation on that of egg development, assuming that the foetus receives reserve from the mother during development at a rate that

Table 1 The 5 budget parameters (upper panel) and 4 variables (lower panel) of the standard DEB model for embryonic development in the length-mass frame

Symbol	Unit	Description
$\dot{v}$	$\mathrm{m\,day^{-1}}$	Energy conductance
g	–	Energy investment ratio
$\dot{k}_J$	$\mathrm{day^{-1}}$	Maturity maintenance rate coefficient
$\dot{k}_M$	$\mathrm{day^{-1}}$	Somatic maintenance rate coefficient
κ	–	Allocation fraction to soma
a, a_b	day	Age, at birth
L, L_b	m	Structural length, at birth
U_H, U_H^b	$\mathrm{day\,m^2}$	Scaled maturity, at birth
U_E, U_E^0, U_E^b	$\mathrm{day\,m^2}$	Scaled reserve, at the start, at birth

The values of the variables at birth are also indicated; U_H^b and $U_E^b L_b^{-3}$ serve as parameters. The value of U_E at the start is indicated, while that of a and U_H are zero at the start. The values U_E^0, U_E^b, a_b and L_b are functions of the $5 + 2$ parameters; this paper aims to identify these functions from the model structure. Dots above symbols mean "per time"

no longer restricts development. In DEB theory, this has the consequence that foetal weight becomes proportional to cubed age, a well-known empirical finding [13] that has astonishing accuracy [19, Fig. 3.18]. In other words, most of the complexity of egg development in DEB theoretic context results from the deceleration of development due to depletion of reserve towards the end of incubation.

Table 1 presents the variables and parameters of the standard DEB model for the embryonic stage. Two parameters deserve extra discussion in the context of this paper: the somatic and maturity maintenance rate coefficients. The somatic maintenance rate coefficient $\dot{k}_M$ has the interpretation of the ratio of the structure-specific somatic maintenance cost and the cost for the synthesis of a unit of structure; the somatic maintenance cost is assumed to be proportional to the amount of structure (in all stages). Likewise the maturity maintenance rate coefficient $\dot{k}_J$ is the ratio of the maturity-specific maturity maintenance cost and the cost for a unit of maturity; the maturity maintenance cost is assumed to be proportional to the level of maturity. Maturity represents information, and not mass or energy; physiologically it stands for a set of regulation systems that structures the various metabolic activities in an individual. If the individual dies, no mass or energy is released from the maturity of the corpse; it simply becomes lost. We avoid quantification of information, however. Maturity is quantified as the cumulative investment of reserve into maturity, but after having increased maturity, the invested reserve is excreted into the environment in decomposed form. I treat $\dot{k}_J$ as a primary parameter. If the maintenance ratio $k = \dot{k}_J/\dot{k}_M$ equals one, maturity is proportional to the amount of structure in the embryonic and juvenile stages and the structure-specific maturity maintenance cost is constant; [19] worked with this parameter to avoid discussing the concept "information". For $k \neq 1$ the use of the structure-specific maturity maintenance cost is no longer handy, however, because is not constant.

The weight of an egg typically changes during development due to loss of water in terrestrial environments (some 10% in birds), or uptake of water in aquatic environments (some factor 8 in daphnids). Reptile eggs manage to take up water in terrestrial environments [4]. I avoid dealing with these changes, using mass of reserve and structure, excluding contributions by water. Apart from these changes in the amount of water, eggs loose mass because of the use of reserve for maintenance, growth and maturation.

The parameter values are individual-specific, but the differences between individuals of the same species are usually small compared to the differences in nutritional condition, especially if eggs are compared of different clutches, environments and/or years. The most likely value to differ among eggs of the same species in the context of DEB theory is the reserve density at birth. The significance of the theory presented in this paper is the implied prediction for how age at birth, weight at birth and initial weight covary as a result of the variation in the reserve density at birth. This covariation can be used to yield information about parameter values.

Although the model is still identical to the original one (and the notation changed little only during 30 years of research on DEB theory), this presentation differs by the variables scaled reserve $U_E = M_E/\{\dot{J}_{EAm}\}$ and scaled maturity $U_H = M_H/\{\dot{J}_{EAm}\}$, where M_E and M_H stand for the mass of reserve and maturity, and $\{\dot{J}_{EAm}\}$ for the surface area-specific maximum reserve assimilation rate. Although the variables might not have a straightforward intuitive interpretation, this scaling is done to avoid the introduction of mass or energy, so that the whole discussion can be confined to the dimensions length and time. This not only simplifies the theoretical discussion, but also the procedure to extract parameter values from experimental data (see the Sect. 7).

In mathematical terms, the standard DEB model for the change in embryonic age a, scaled reserve U_H, length L and scaled maturity U_H amounts to

$$\frac{d}{da}U_E = -S_C \quad \text{with } S_C = L^2\frac{ge}{g+e}\left(1+\frac{\dot{k}_M L}{\dot{v}}\right) \quad \text{and} \quad e \equiv \frac{U_E\dot{v}}{L^3} \tag{1}$$

$$\frac{d}{da}L = \frac{\dot{v}e - \dot{k}_M g L}{3(e+g)} \tag{2}$$

$$\frac{d}{da}U_H = (1-\kappa)S_C - \dot{k}_J U_H \tag{3}$$

where the variable (U_E, L, U_H) evolves from value $(U_E^0, 0, 0)$ at $a = 0$ to value (U_E^b, L_b, U_H^b) at $a = a_b$, which is at birth. Apart from the five parameters $\dot{k}_M$, $\dot{k}_J$, $\dot{v}$, g, κ, only the scaled maturity at birth U_H^b and the (dimensionless) scaled reserve density at birth $e_b = \dot{v}U_E^b L_b^{-3}$ are given and the problem is to find U_E^0 and so a_b, U_E^b and L_b. For the special case $k = 1$ (i.e. $\dot{k}_J = \dot{k}_M$), the solution is given in [19], but the present problem is to find expressions for the general case that $k \neq 1$.

All symbols in this paper stand for real non-negative quantities; the biologically meaningful ranges, as deduced from the model structure, are $e > e_b$ and $e_b < 1$ and $0 < l < l_b < e_b$ and $0 < U_H < U_H^b < \frac{(1-\kappa)v^2}{g^2\dot{k}_M^3}$ and $0 < \kappa < 1$ and $0 < k < \frac{(1-e_b)e_b^3\dot{v}}{U_H^b g^2 \dot{k}_M^2}$.

Table 2 The definitions for the dimensionless scaled variables and parameters that are used to find the initial amount of scaled reserve $u_E^0 = U_E^0 g^2 \dot{k}_M^3/\dot{v}^2$

$\tau = a\dot{k}_M$	$\tau_b = a_b\dot{k}_M$	$l = Lg\dot{k}_M/\dot{v}$	$l_b = L_b g\dot{k}_M/\dot{v}$
$u_E = U_E g^2 \dot{k}_M^3/\dot{v}^2$	$u_E^b = U_E^b g^2 \dot{k}_M^3/\dot{v}^2$	$u_H = U_H g^2 \dot{k}_M^3/\dot{v}^2$	$u_H^b = U_H^b g^2 \dot{k}_M^3/\dot{v}^2$
$e = gu_E/l^3$	$e_b = gu_E^b/l_b^3$	$e_H = gu_H/l^3$	$e_H^b = gu_H^b/l_b^3$
$x = \frac{g}{e+g}$	$x_b = \frac{g}{e_b+g}$	$\alpha = 3gx^{1/3}/l$	$\alpha_b = 3gx_b^{1/3}/l_b$
$y = \frac{xe_H}{1-\kappa}$	$y_b = \frac{x_b e_H^b}{1-\kappa} = gx_b v_H^b l_b^{-3}$	$k = \dot{k}_J/\dot{k}_M$	$v_H^b = \frac{u_H^b}{1-\kappa}$

3 Initial amount of reserve and age, length at birth

The key to finding the cost of an egg is finding an appropriate scaling of variables for solving the boundary value problem. Table 2 shows the scaled variables. I first remove 2 parameters by scaling the variable (a, U_E, L, U_H) to the dimensionless variable (τ, u_E, l, u_H) or, alternatively, to the dimensionless variable (τ, e, l, e_H). This is possible because the original problem has dimensions length and time, which can be eliminated.

The reformulated problem is now: find τ_b, l_b, u_E^0 given u_H^b, k, g, κ and $u_E^b = e_b l_b^3/g$. We also have $0 < k < (1-\kappa)e_b^3/u_H^b$ and $u_H^b < 1-\kappa$.

For the variable (τ, u_E, l, u_H) evolving from the value $(0, u_E^0, 0, 0)$ to the value $(\tau_b, u_E^b, l_b, u_H^b)$, the scaled model amounts to

$$\frac{d}{d\tau}u_E = -u_E l^2 \frac{g+l}{u_E + l^3} \tag{4}$$

$$\frac{d}{d\tau}l = \frac{1}{3}\frac{gu_E - l^4}{u_E + l^3} \tag{5}$$

$$\frac{d}{d\tau}u_H = (1-\kappa)u_E l^2 \frac{g+l}{u_E + l^3} - ku_H \tag{6}$$

or alternatively for variable (τ, e, l, e_H) evolving from the value $(0, \infty, 0, e_H^0)$ to the value $(\tau_b, e_b, l_b, e_H^b)$

$$\frac{d}{d\tau}e = -g\frac{e}{l} \tag{7}$$

$$\frac{d}{d\tau}l = \frac{g}{3}\frac{e-l}{e+g} \tag{8}$$

$$\frac{d}{d\tau}e_H = (1-\kappa)\frac{ge}{l}\frac{l+g}{e+g} - e_H\left(k + \frac{g}{l}\frac{e-l}{e+g}\right) \tag{9}$$

where $e_H^0 = (1-\kappa)g$ is such that $\frac{d}{d\tau}e_H(0) = 0$, else $\frac{d}{d\tau}e_H(0) = \pm\infty$. If $k = 1$ we have $e_H(\tau) = e_H^0$ for all τ and $u_H(\tau) = (1-\kappa)l_b^3$. For $k > 1$, e_H is decreasing in (scaled) age, and for $k < 1$ increasing.

Before I derive expressions for τ_b, u_E^0 and l_b, I first make an observation on α (see Table 2) that is used later.

From Table 2 and ode's Eqs. (7–8), we have

$$\frac{d}{d\tau}x = gx\frac{1-x}{l} \tag{10}$$

$$\frac{d}{d\tau}l = \frac{g - xg - lx}{3} \tag{11}$$

$$\frac{d}{d\tau}\alpha = \frac{x^{1/3}}{1-x}\frac{d}{d\tau}x \tag{12}$$

so

$$\alpha = 3g(u_E^0)^{-1/3} + B_x\left(\frac{4}{3}, 0\right) \tag{13}$$

where $B_x(a,b) \equiv \int_0^x y^{a-1}(1-y)^{b-1}\,dy$ is the incomplete Beta function, which reduces for this particular case to

$$B_x\left(\frac{4}{3}, 0\right) = \sqrt{3}\left(\arctan\frac{1+2x^{1/3}}{\sqrt{3}} - \arctan\frac{1}{\sqrt{3}}\right) + \frac{1}{2}\log(1 + x^{1/3} + x^{2/3}) - \log(1 - x^{1/3}) - 3x^{1/3}.$$

Consequently we have

$$\alpha_b - \alpha = B_{x_b}\left(\frac{4}{3}, 0\right) - B_x\left(\frac{4}{3}, 0\right) \tag{14}$$

$$\frac{1}{l} = \frac{1}{l_b}\left(\frac{x_b}{x}\right)^{1/3} - \frac{B_{x_b}(\frac{4}{3}, 0) - B_x(\frac{4}{3}, 0)}{3gx^{1/3}} \tag{15}$$

We need this expression for $l(x)$ later in the derivation of l_b.

I now first derive expressions for τ_b and u_E^0 assuming that l_b is known, and then I derive an expression for l_b.

3.1 Scaled age at birth τ_b

The scaled age at birth τ_b follows from Eqs. (10) and (15) by separation of variables and integration

$$\tau_b = 3\int_0^{x_b} \frac{dx}{(1-x)x^{2/3}(\alpha_b - B_{x_b}(\frac{4}{3}, 0) + B_x(\frac{4}{3}, 0))} \tag{16}$$

Equation (16) is consistent with the one for $k = 1$ [19, Eq. (3.33)], but l_b in α_b is not a parameter and given below.

3.2 Scaled initial amount of reserve u_E^0

The scaled initial amount of reserve u_E^0 directly follows from Eq. (13) for $x = x_b$ and $\alpha = \alpha_b$

$$u_E^0 = \left(\frac{3g}{\alpha_b - B_{x_b}\left(\frac{4}{3}, 0\right)} \right)^3 \tag{17}$$

Equation (17) is consistent with the one for $k = 1$ [19, Eq. (3.31)], but l_b in α_b is not a parameter and given below.

3.3 Scaled length at birth l_b

The *pièce de resistance* for solving our boundary value problem is finding l_b, which turns out to be rather straightforward once the appropriate transformation of variables is found (namely $y(x)$, see Table 2). For the variable (τ, x) evolving from the value $(0, 0)$ to the value (τ_b, x_b) and the variable (τ, e_H) evolving from the value $(0, e_H^0)$ to the value (τ_b, e_H^b) we have the ode for x, Eq. (10), and

$$\frac{d}{d\tau} e_H = (1-\kappa) g (1-x) \left(\frac{g}{l(x)} + 1 \right) - e_H \left(k - x + g \frac{1-x}{l(x)} \right)$$

Now consider the variable (x, e_H) evolving from the value $(0, e_H^0)$ to the value (x_b, e_H^b) or the variable (x, y) evolving from the value $(0, 0)$ to the value (x_b, y_b):

$$\begin{aligned} &\frac{d}{dx} e_H = \frac{e_H^0}{x} \left(\frac{l(x)}{g} + 1 \right) - \frac{e_H}{x} \left(\frac{k-x}{1-x} \frac{l(x)}{g} + 1 \right) \quad \text{for } e_H^0 = e_H(0) = (1-\kappa) g \\ &\frac{d}{dx} y = r(x) - y s(x) \quad \text{for } r(x) = g + l(x); \quad s(x) = \frac{k-x}{1-x} \frac{l(x)}{gx} \end{aligned} \tag{18}$$

where $l(x)$ is given in Eq. (15). The ode for y can be solved to

$$y(x) = v(x) \int_0^x \frac{r(x_1)}{v(x_1)} dx_1 \quad \text{with } v(x) = \exp\left(- \int_0^x s(x_1)\, dx_1 \right)$$

The quantity l_b must be solved from $y_b = y(x_b) = g x_b v_H^b l_b^{-3}$, see Table 2. So we need to find the root of t as function of l_b with

$$t(l_b) = \frac{x_b g v_H^b}{v(x_b) l_b^3} - \int_0^{x_b} \frac{r(x)}{v(x)} dx = 0 \tag{19}$$

From this equation it becomes clear that the parameters κ and u_H^b affect l_b only via $v_H^b = \frac{u_H^b}{1-\kappa}$; a conclusion that is more difficult to obtain using the ode for the scaled maturity density e_H rather than that for abstract variable y. Notice that the solution of l_b (and that of u_E^0 and τ_b) for the boundary value problem for the ode for (u_E, l, e_H) as given in Eqs. (4–6) depends on the four parameters g, k, v_H^b and e_b only. The solution for l_b must be substituted into Eq. (17) to obtain u_E^0 and in Eq. (16) to obtain τ_b; the scaled reserve at birth is $u_E^b = e_b l_b^3/g$.

3.4 Numerical solution for scaled length at birth l_b

This subsection discusses numerical methods to obtain the root of function t as given in Eq. (19). The shooting method (in one dimension) on the ode for y, Eq. (18), turns out to be rather stable, where $y(x_b) = y_b$ is evaluated by integrating $\frac{d}{dx}y$ using $l_b = \left(v_H^b\right)^{1/3}$ as starting value, which is the exact solution for $k = 1$. Since l_b is a scaled length, v_H^b has the interpretation of a scaled volume, which has been the motivation for the choice of the symbol.

Alternatively the Newton–Raphson procedure $l_b^{i+1} = l_b^i - t(l_b^i)/t'(l_b^i)$ can be used to solve Eq. (19) with

$$l(x) = \left(\frac{1}{l_b}\left(\frac{x_b}{x}\right)^{1/3} - \frac{B_x(\frac{4}{3},0) - B_{x_b}(\frac{4}{3},0)}{3gx^{1/3}}\right)^{-1}; \quad l'(x) = \frac{l^2(x)}{l_b^2}\left(\frac{x_b}{x}\right)^{1/3}$$

$$v(x) = \exp\left(-\int_0^x \frac{k-x_1}{1-x_1}\frac{l(x_1)}{g}\frac{dx_1}{x_1}\right); \quad v'(x) = v(x)\exp\left(-\int_0^x \frac{k-x_1}{1-x_1}\frac{l'(x_1)}{g}\frac{dx_1}{x_1}\right)$$

$$r(x) = g + l(x); \quad r'(x) = l'(x)$$

$$t(l_b) = \frac{x_b g u_H^b}{(1-\kappa)v(x_b)l_b^3} - \int_0^{x_b} \frac{r(x)}{v(x)}dx$$

$$t'(l_b) = -\frac{x_b g u_H^b}{(1-\kappa)v(x_b)l_b^3}\left(\frac{3}{l_b} + \frac{v'(x_b)}{v(x_b)}\right) - \int_0^{x_b}\left(\frac{r'(x)}{r(x)} - \frac{v'(x)}{v(x)}\right)\frac{r(x)}{v(x)}dx$$

The problem here is in the accurate evaluation of the integrals. Euler integration requires a fine grid if $k \gg 1$, but the combination of the Newton–Raphson method and the Euler integration is nonetheless much faster than the shooting method, especially if started for the l_b of the foetus. Moreover, data indicates that $k < 1$ is more typical in practice.

3.5 Special case $e \to \infty$: foetal development

The special case $e \to \infty$, which is approximative for foetal development, makes that $\frac{d}{d\tau}l = g/3$, or $l(\tau) = g\tau/3$. We further have

$$\frac{d}{d\tau}u_H = (1-\kappa)l^2(g+l) - ku_H$$

$$u_H(\tau) = \frac{g^3(1-\kappa)}{3^3k^4}\left(k^2\tau^2(3k+k\tau-3) + 6(k-1)(1-\tau-\exp(-k\tau))\right)$$

The equation $u_H(\tau_b) = u_H^b$ has to be solved numerically for τ_b, but for $k = 1$ we have $u_H^b = (1-\kappa)3^{-3}g^3\tau_b^3 = (1-\kappa)l_b^3$, from which τ_b can be solved easily and be used as a starting value for the case $k \neq 1$. The solution of this equation is stable and fast; the resulting scaled length at birth $l_b = g\tau_b/3$ can be used to start the Newton–Raphson procedure to find l_b for an egg. This start is preferable if k is substantially different from 1. From $l_b < 1$, so $\tau_b < 3/g$, we can derive the constraint

$$\frac{k^2u_H^b}{1-\kappa} < k + g(k-1) + g^3\frac{k-1}{k^2}\,\frac{1-3/g-\exp(-3k/g)}{9/2}$$

It can be shown that $1 < \frac{g\tau_b}{3l_b} < 1 + \frac{g}{e_b}$ generally holds, see [23]; the range in the foetus case being restricted to zero ($e_b \to \infty$).

For $u_E^b = u_E(\tau_b)$, the cost for a foetus amounts to

$$u_E^0 = u_E^b + \kappa l_b^3 + u_H^b + \int_0^{\tau_b}(\kappa l^3(\tau) + ku_H(\tau))\,d\tau = u_E^b + l_b^3 + \frac{3}{4}\frac{l_b^4}{g} \qquad (20)$$

where the five terms correspond with the costs of reserve, structure, maturity, somatic and maturity maintenance, respectively. The second equality follows from the structure of DEB theory; the investment in maturity plus maturity maintenance equals $\frac{1-\kappa}{\kappa}$ times the investment in structure plus somatic maintenance and $l(\tau) = g\tau/3$. The cost of a foetus as given in Eq. (20) is somewhat smaller than that of an egg as given in Eq. (17), because development decelerates towards the end of incubation; the structure has to be maintained over a longer period.

4 Body size scaling relationships

DEB theory implies rules for how the primary parameters of the standard model covary among species [17,20,34], generally known as body-size scaling relationships where the variation of parameter values are studied as function of the maximum structural length of a species, $L_m = \frac{\dot{v}}{g\dot{k}_M}$ [19, p. 94], which is defined as the cubic root of the maximum structural volume. In the DEB theory this length is a compound parameter, so a consequence of underlying processes (assimilation, allocation and maintenance), rather than a basic quantity. This section discusses some of the (compound) parameters of the standard DEB model as function of the (dimensionless) zoom factor z, which is the maximum structural length of a species, relative to a reference value. The maintenance rate coefficients $\dot{k}_J$ and $\dot{k}_M$, the energy conductance $\dot{v}$ and the allocation fraction κ are independent of the zoom factor. This implies that the energy investment ratio g

tends to covary inversely to the zoom factor. The scaled maturity at birth U_H^b covaries with the squared zoom factor. This is because the (unscaled) maturity at birth $M_H^b = U_H^b\{\dot{J}_{EAm}\}$ covaries with the cubed zoom factor, and the surface area specific reserve assimilation rate $\{\dot{J}_{EAm}\}$ covaries with the zoom factor. The energy investment ratio g is a compound parameter, which has $\{\dot{J}_{EAm}\}$ is its denumerator and so covaries with the inverse zoom factor [19, p. 270].

These variations of parameter values among species determine how functions of these parameters, such as length and age at birth, and initial amount of reserve covary with maximum length. Parameter values that quantify metabolic traits are rather predictable, while life history parameters, such as the maturity at birth, are highly adaptable (from an evolutionary point of view). Within particular taxa the variation is less, however. The primary parameter that is in control of length at birth is the maturity at birth. Previously [18, p. 283] I discussed the logic behind the relatively small egg size of the (European) cuckoo, as an adaptation to match the incubation time of the eggs of its much smaller host, and the relatively large eggs of the tube-noses (*Procellariformes* to which albatrosses belong) as an adaptation to shorten the time that they are bound to a particular nesting site. Like the more general classification of birds (and other taxa) in altricial and precocial ones, variation in the maturity at birth is the key to understand these patterns in the context of DEB theory, and I am still behind this point of view. I will now discuss another source of variation of relative egg size, cq length at birth, that is new and deserves noticing.

Figure 2 shows the scaled initial amount of reserve, and the scaled length and scaled age at birth as a function of the zoom factor for a large range of 10^4. If $k = 1$ and $\alpha_b >> B_{x_b}(\frac{4}{3}, 0)$, the initial reserve scales approximately with the zoom factor to the power 4. The scaled initial reserve u_E^0 scales, therefore, scales with the zoom factor, which is confirmed in the figure. If $k = 1$, the structural volume at birth is proportional to the maturity at birth, so length at birth scales with the zoom factor, which means that scaled length is independent of the zoom factor. If $k = 1$ age at birth, and therefore also scaled age at birth, scales with the zoom factor [18]. These results are known for two decades now [18], but now shown for scaled variables to study the effect for $k \neq 1$.

The scaling is more complex if $k \neq 1$, especially for the length at birth and the initial reserve; I presented the approximate scaling exponents to comply with the traditional way to present these types of relationships. It is remarkable that taxa show a wide scatter in scaling relationships for specially these quantities (as well as the length at puberty, which is not discussed in this paper). This suggests that taxa might differ in the maintenance ratio. The increase in the maintenance ratio k goes with an increase in the relative size at birth for any given value of the zoom factor, but the effect is bigger for the large-bodied species. Since protein turnover is an important component of somatic maintenance costs, and activity is typically a minor component, it is not likely that species differ a lot in the somatic maintenance costs. I expect that the cost for defence (e.g. the immune system) varies more among species. It is tempting to speculate about the relatively small egg size of dinosaurs (indicating small maturity maintenance costs) versus the relatively large size at birth of mammals (indicating high maturity maintenance costs).

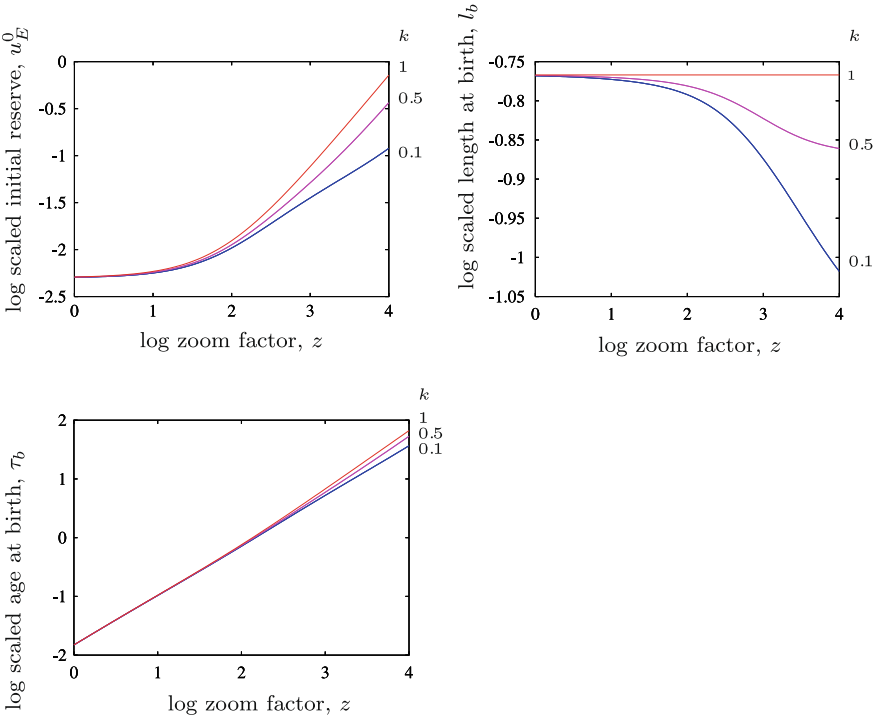

Fig. 2 The scaled initial reserve (*left*), length at birth (*middle*), and age at birth (*right*) as function of the zoom factor, log–log plotted (base 10). Each plot has three curves, corresponding to maintenance ratio $k = 0.1$ (*lower*), 0.5 (*middle*), 1 (*upper*). Parameters: $g = 80/z$, $u_H^b = 0.005$, $e_b = 1$. The curves are approximately allometric with slopes for large zoom factors

Maintenance ratio k	0.1	0.5	1.0
Scaled initial reserve u_E^0	0.55	0.83	1.00
Scaled length at birth l_b	−0.14	−0.04	0.00
Scaled age at birth τ_b	0.85	0.89	0.93

5 Separation of cells in the two or four-cell stage

Suppose that the cells in the two-cell stage of an embryo are identical in terms of amounts of maturity, reserve and structure. If the cells are separated, the three amounts are halved. It is not obvious from the definition of maturity that maturity of the daughter cells is half of that of the mother, but since the two-cell stage is very early in the development, so the maturity level is very small, this problem is numerically not important. Figure 3 shows the expected results of such an event, which sometimes occurs spontaneously. The plots for maturity and structural volume are almost identical in this case because $\dot{k}_J/\dot{k}_M$ is very close to 1; the maturity density then remains constant.

The parameter values for *Daphnia magna* at 20°C are $U_H^b = 0.012\,\mathrm{d\,mm^2}$, $g = 0.422$, $\dot{k}_J = 1.70\ \mathrm{d}^{-1}$, $\dot{k}_M = 1.71\ \mathrm{d}^{-1}$, $\dot{v} = 3.24\ \mathrm{mm\,d}^{-1}$, which gives a scaled maturity maintenance rate of $k \simeq 1$ and a scaled maturity at birth of $u_H^b = 0.001$ [23].

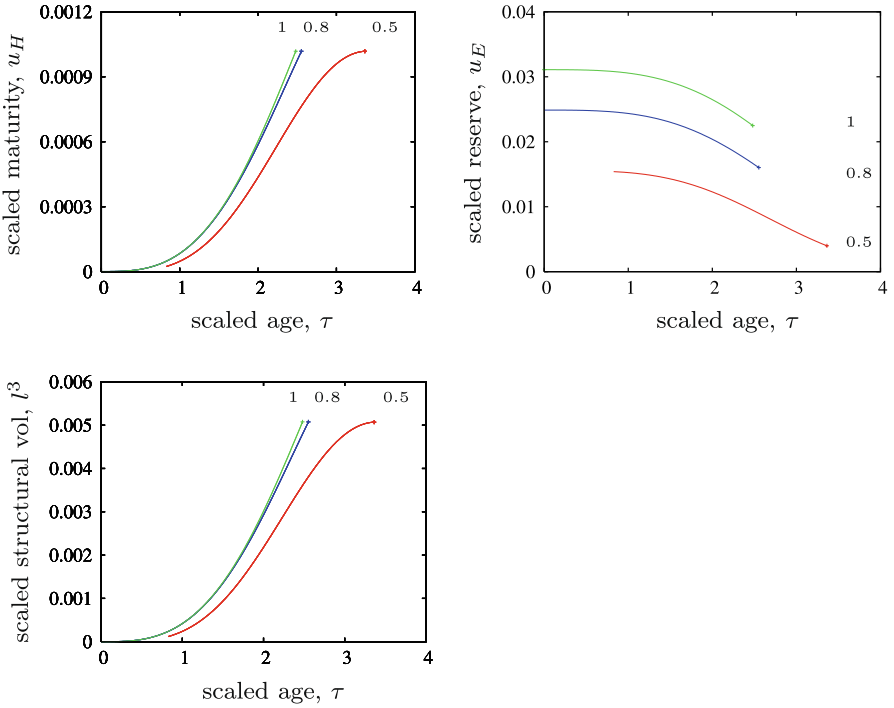

Fig. 3 The scaled maturity (*left*), reserve (*middle*), and structural volume (*right*) during embryonic development. Each plot has three curves, corresponding with a reduction of the reserve, structure and maturity by factor 1, 0.8 and 0.5. Multiplication by 1 represents the "blank" situation. Multiplication by 0.8 at $\tau = 0$ represents a (small) reduction of the initial amount of reserve, and by a factor 0.5 at $\tau = \tau_b/3$ a separation of cells in the two-cell stage. The age of this stage is here chosen arbitrarily. Parameters: $\kappa = 0.8$, $g = 0.422/1.87$, $k = 0.99415$; $u_H^b = 0.001$, $e_b = 1$. The parameter values are chosen such that the twins cease maturation at birth. (The 0.5-curve in the first graph has tangent zero at $\tau = \tau_b$.) Given the values for κ, k and u_H^b only species with a smaller value for g can successfully separate cells in the two-cell stage

If one would try to separate cells in this species, the theory predicts that the initial reserve is not enough the cover embryonic development. This result is remarkable because these parameters imply that a fraction of 0.63 of the initial amount of reserve is still left at birth at abundant food, see [23]. The explanation is that the mobilisation of reserve decreases with the reserve density. It might be, of course, that maturity at birth is affected by cell separation, which can still allow this to occur successfully in small-bodied species. However, I am unaware of any empirical evidence for this.

The reserve density capacity $[E_m] = \{\dot{J}_{EAm}\}/\dot{v}$ scales with the zoom factor. So species with a larger ultimate body size tend to have a relatively larger reserve capacity. It turned out that for the combination of parameter values as found for *D. magna* we have to reduce g be a factor of at least $z = 1.87$ to arrive at a minimum maximum body size for which cell separation might be successful. Figure 3 illustrates embryo development with this reduced value for g, where maturation ceases at birth. Since k is close to 1, this almost coincides with the condition that growth ceases at birth. This is a worst case situation because abundant food conditions are used ($e_b = 1$) for the

maternal effect. Successful cell separation at lower food densities for the mother can only occur in even larger species (so smaller values for g).

For $k > 1$, the structural volume at birth increases after halving, and decreases for $k < 1$. Since reserve contributes to weight, the weight at birth is close to half of the original weight at birth, irrespective of the value of k. The age of the two-cell stage is probably smaller than $\tau_b/3$, but the results are not sensitive to this choice.

Hart [11] studied the effect of separation of the embryonic cells of the sea urchin *Strongylocentrotus droebachiensis* in the two-cell stage on the energetics of larval development. Both the size and the feeding capacity of the resulting larva were reduced by about one-half, but the time to metamorphosis is about the same (7 days at 8–13°C). The maximum clearance rate of dwarf and normal larvae was found to be the same function of the ciliated band length. Larvae fed at smaller ration had longer larval periods, but food ration hardly affected size at metamorphosis. Egg size affected juvenile test diameter only slightly. These qualitative observations are consistent with the standard DEB model for $k < 1$, which results in a reduced size at birth, while feeding rate is proportional to surface area.

A full treatment of the effect of cell separation on size at birth for foetal development is beyond the scope of this paper. Ignoring effects of endothermy, a simple application can illustrate how the theory works in practice. Armadillo's typically separate cells in the four-cell stage of the embryo, giving birth to four identical offspring. Humans rarely do this successfully, then giving birth to four babies of about 1 kg each, rather than the typical 3 kg. In terms of an effect on length this reduction amounts to a factor $(1/3)^{1/3} = 0.69$. The human growth curve fits the von Bertallanffy curve very well, with a von Bertalanffy growth rate of $\dot{r}_B = \frac{\dot{k}_M g}{3(e+g)} = 0.123$ a^{-1} [19, p. 262]. We can safely assume that the scaled reserve density was close to its maximum $e = 1$ for the post-embryonic stages. Moreover, the age at birth is $a_b = \frac{3 l_b}{g \dot{k}_M} = 0.75$ a for humans. If we take a typical maximum adult weight of 70 kg, then the scaled length at birth equals $l_b = (3/70)^{1/3} = 0.35$. So the energy investment ratio equals $g = \frac{l_b}{a_b \dot{r}_B} - 1 = 2.79$, the somatic maintenance rate coefficient $\dot{k}_M = \frac{3 l_b}{g a_b} = 0.5$ a^{-1} and the scaled age at birth $\tau_b = a_b \dot{k}_M = 0.375$. With these values for g, e_b and l_b, the scaled cost amounts to $u_E^0 = 0.062$ from Eq. 20. In the case of 4 babies with a reduced length by a factor 0.69, the scaled cost per baby equals $u_E^0 = 0.02$, so summed over the 4 babies this is 1.3 times the amount of a single baby; not a surprising result, in view of the 4 kg of babies relative to the 3 kg for a single baby.

6 Removal of some initial reserve

To simulate effects of caloric restriction of the mother on embryo development, researchers sometimes remove an amount of reserve at the start of the development, e.g. [7,15,16,27,33]. Figure 3 shows the expected results, namely an elongation of the incubation time, and a reduction of the reserve at birth. The pattern is rather similar to that of the separation of cells at an early stage, because reductions of structure and maturity at an early stage have little effect. Although not very obvious in these plots, the initial amount of reserve is a U-shaped function of the reserve at birth. The right

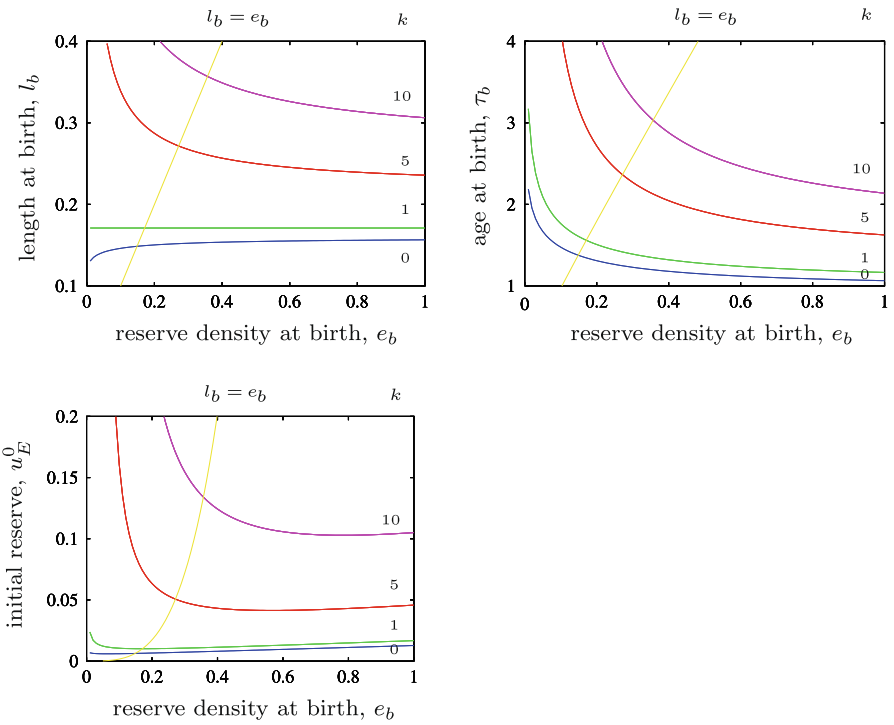

Fig. 4 The scaled length at birth (*left*), age at birth (*middle*), and initial reserve (*right*) as function of the scaled reserve at birth for various values of k. The length, age and reserve at $l_b = e_b$ is also indicated; the structure is shrinking at birth for smaller values of e_b, so smaller values [i.e. *left* of the ($l_b = e_b$)-curve] hardly have biological meaning. Parameters: $\kappa = 0.8$, $g = 0.5$, $u_H^b = 0.001$

branch is explained by the larger amount of reserve at birth, the left branch by the larger age at birth, which comes with larger cumulative somatic maintenance requirements.

A reduction of the initial amount of reserve comes with an increase of the age at birth, see Fig. 4. This has been observed in e.g. the gypsy moth [32]. Crested penguins sport egg size dimorphy [35]. The standard DEB model correctly predicts that, although the 1.5 times larger egg is produced some days later, it hatches first, if fertile. Figure 4 shows little variation of (scaled) length at birth for $k < 1$. The variation is larger, however, for larger values of u_H^b. The size of neonates of trout and salmon, was found to increase with the initial egg size [6,12], suggesting that $k < 1$ for samonids. This also applies to the emu [5], and probably represents a general pattern.

7 Discussion

The standard DEB model implies von Bertalanffy growth curves for post-embryonic stages at constant food levels. Its three parameters at several (>1) food levels, in combination with the length at puberty and the maximum reproduction rate (so for a fully grown adult) at abundant food, determine the values of seven parameters: allocation fraction κ, energy investment ratio g, maturity maintenance rate coefficient

$\dot{k}_J$, somatic maintenance rate coefficient $\dot{k}_M$, energy conductance $\dot{v}$, scaled maturity at birth U_H^b, scaled maturity at puberty U_H^p [23]. I here provided an efficient algorithm to obtain the scaled initial reserve U_E^0 and age at birth a_b from six of the seven parameters. This is remarkable, because no measurements of food intake are required, for instance, to access the scaled cost of eggs. No advanced data is required for practical application of the theory.

The significance of this for energetics is that, in combination with the measured initial mass M_E, the scaled initial amount of reserve U_E^0 gives access to the surface area specific maximum assimilation flux $\{\dot{J}_{EAm}\} = M_E^0/U_E^0$ [23]. Knowledge about this key parameter is essential to make the step from compound to primary DEB parameters. In combination with the measured maximum surface area-specific food uptake rate $\{\dot{J}_{XAm}\}$, the digestion efficiency yields, for instance, via $y_{EV} = \{\dot{J}_{EAm}\}/\{\dot{J}_{XAm}\}$. This procedure circumvents the problem of accessing the digestion efficiency via the difference of ingested food and excreted faeces: the gut micro-flora takes its share, so part of the difference never entered the animal. In combination with the measured mass at birth, knowledge of U_E^0 gives access to the yield of structure on reserve y_{VE}, see [23]. These applications of the theory show that the embryo can reveal valuable information about the juvenile and adult stages, as the title suggests.

The relationship between the initial amount of reserve and budget parameters has many consequences, and some of them are quite unexpected (at least for me). Some toxic compounds, for instance, have the effect of increasing the cost of synthesis of structure, which is a component of the energy investment ratio g. This has the indirect effect of decreasing the allocation to reproduction, since food uptake increases with size over the life cycle. However, it also reduces the initial amount of reserve (by decreasing the amount of structure at birth). This has the overall effect that the reproduction rate, i.e. the ratio of the reserve allocated to reproduction and the initial amount of reserve, can increase for increasing concentrations of toxic compound, as long as these concentrations are low. This seemingly stimulating effect on reproduction that some toxic compounds can have at low concentrations is well know in practice, especially in the *Daphnia* reproduction test, as standardised by the OECD and the ISO [21,22]. The phenomenon is known as hormesis, but the mechanisms are typically enigmatic. The present analysis reveals a potential mechanism that needs experimental verification.

All computations that are discussed in this paper have been included in the freely down-loadable package DEBtool (Octave and Matlab): http://www.bio.vu.nl/thb/deb/deblab/debtool. Toolbox `animal` has functions `get_lb`, `get_ue0` and `get_tb` to obtain l_b, u_E^0 and τ_b from κ, k, u_H^b g and e_b. Earlier versions of DEBtool used a shooting method for (U_E, L, U_H) (so in three dimensions) to find the scaled cost of an egg U_E^0. The substantial computational effort of this method slowed down (parameter estimation) routines that frequently require the evaluation of reproduction rates. On the basis of the results mentioned in this paper these DEBtool routines are now replaced and are both more accurate and orders of magnitude faster, at least for some combinations of parameter values.

Acknowledgments I like to thank the AQUAdeb Group, Odo Diekmann, Roger Nisbet and Tjalling Jager for helpful suggestions and discussions.

References

1. Alda Alvarez, O., Jager, T., Marco Redondo, E., Kammenga, J.E.: Assessing physiological modes of action of toxic stressors with the nematode *Acrobeloides nanus*. Environ. Toxicol. Chem. **25**, 3230–3237 (2006)
2. Benton, T.G., Plaistow, S.J., Beckerman, A.P., Lapsley, C.T., Littlejohns, S.: Changes in maternal investment in eggs can affect population dynamics. Proc. R. Soc. **272**, 1351–1356 (2005)
3. Bertram, D.F., Strathmann, R.R.: Effects of maternal and larval nutrition on growth and form of planktotrophic larvae. Ecology **79**, 315–327 (1998)
4. Deeming, D.C., Birchard, G.F.: Allometry of egg and hatcling mass in birds and reptiles: roles of developmental maturity, eggshell structure and phylogeny. J. Zool. **271**, 78–87 (2007)
5. Dzialowski, E.M., Sotherland, P.R.: Maternal effects of egg size on emu Dromaius novaehollandiae egg composition and hatchling phenotype. J. Exp. Biol. **207**, 597–606 (2004)
6. Einum, S., Fleming, I.A.: Maternal effects of egg size in brown trout (Salmo trutta): norms of reaction to environmental quality. Proc. Biol. Sci. **266**(1433), 2095–2095 (1999)
7. Finkler, M.S., Orman, J.B.v., Sotherland, P.R.: Experimental manipulation of egg quality in chickens: influence of albumen and yolk on the size and body composition of near-term embryos in a precocial bird. J. Comp. Physiol. B **168**, 17–24 (1998)
8. Flye Sainte Marie, J.: Ecophysiology of brown ring disease in the manila clam Ruditapes philippinarum, experimental and modelling approaches. Ph.D. thesis, Brest University and Vrije Universiteit, Brest and Amsterdam (2008)
9. Glazier, D.S.: Effects of food, genotype, and maternal size and age on offspring investment in *Daphnia Magna*. Ecology **73**(3), 910–926 (1992)
10. Gliwicz, Z.M., Guisande, C.: Family planning in *Daphnia*: resistance to stravation in offspring born to mothers grown at different food levels. Oecologia **91**, 463–467 (1992)
11. Hart, M.W.: What are the costs of small egg size for a marine invertebrate with feeding planktonic larvae? Am. Nat. **146**, 415–426 (1995)
12. Heath, D.D., Fox, C.W., Heath, J.W.: Maternal effects on offspring size: variation through early development of chinook salmon. Evolution **53**(5), 1605–1611 (1999)
13. Huggett, A.S.G., Widdas, W.F.: The relationship between mammalian foetal weight and conception age. J. Physiol. (Lond.) **114**, 306–317 (1951)
14. Jager, T., Heugens, E.H.W., Kooijman, S.A.L.M.: Making sense of ecotoxicological test results: towards process-based models. Ecotoxicology **15**, 305–314 (2006)
15. Jardine, D., Litvak, M.K.: Direct yolk sac volume manipulation of zebrafish embryos and the relationship between offspring size and yolk sac volume. J. Fish Biol. **63**, 388–397 (2003)
16. Ji, X., Du, W.G., Xu, W.Q.: Experimental manipulation of eggs size and hatling size in the cobra, Naja naja atra (Elapidae). Neth. J. Zool. **49**, 167–175 (1999)
17. Kooijman, S.A.L.M.: Energy budgets can explain body size relations. J. Theor. Biol. **121**, 269–282 (1986)
18. Kooijman, S.A.L.M.: What the hen can tell about her egg; egg development on the basis of budgets. J. Math. Biol. **23**, 163–185 (1986)
19. Kooijman, S.A.L.M.: Dynamic Energy and Mass Budgets in Biological Systems. Cambridge University Press, Cambridge (2000)
20. Kooijman, S.A.L.M., Baas, J., Bontje, D., Broerse, M., Jager, T., Gestel, C.v., Hattum, B.v.: Scaling relationships based on partition coefficients and body sizes have similarities and interactions. SAR and QSAR in Environ. Res. (2007)
21. Kooijman, S.A.L.M., Bedaux, J.J.M.: Analysis of toxicity tests on Daphnia survival and reproduction. Water Res. **30**, 1711–1723 (1996)
22. Kooijman, S.A.L.M., Bedaux, J.J.M., Péry, A.R.R., Jager, T.: Biology-based methods. In: Magaud, H. (ed.) Current Approaches in the Statistical Analysis of Ecotoxicity Data: A Guidance to Application. Series on Testing Assessment, vol. 54, TC 147/ SC 5/ WG 10/ N0390, Chap. 7. ISO and OECD, Paris (2006)
23. Kooijman, S.A.L.M., Sousa, T., Pecquerie, l., Meer, J.v.d., Jager, T.: From food-dependent statistics to metabolic parameters, a practical guide to the use of dynamic energy budget theory. Phil. Trans. R. Soc. B (submitted) (2008)
24. Kooijman, S.A.L.M., Troost, T.A.: Quantitative steps in the evolution of metabolic organisation as specified by the dynamic energy budget theory. Biol. Rev. **82**, 1–30 (2007)

25. Loman, J.: Microevolution and maternal effects on tadpole Rana temporaria growth and development rate. J. Zool. **257**(01), 93–99 (2002)
26. McIntyre, G., Gooding, R.: Egg size, contents, and quality: maternal-age and-size effects on house fly eggs. Can. J. Zool./Rev. Can. Zool **78**(9), 1544–1551 (2000)
27. Morley, S.A., Batty, R.S., Geffen, A.J., anf Tytler, P.: Egg size manipulation: a technique for investigating maternal effects on the hatching characteristics of herring. J. Fish Biol. **55**(suppl A), 233–238 (1999)
28. Nager, R.G., Monaghan, P., Houston, D.C.: Within-clutch trade-offs between the number and quality of eggs: experimental manipulations in gulls. Ecology **81**, 1339–1350 (2000)
29. Nager, R.G., Monaghan, P., Houston, D.C., Arnold, K.E., Blount, J.D., Berboven, N.: Maternal effects through the avian egg. Acta Zool. Sin. **52**(suppl), 658–661 (2006)
30. Reznick, D., Callahan, H., Llauredo, R.: Maternal effects on offspring quality in poeciliid fishes. Integr. Comp. Biol. **36**(2), 147 (1996)
31. Rossiter, M.C.: Environmentally-based maternal effects: a hidden force in insect population dynamics? Oecologia **87**(2), 288–294 (1991)
32. Rossiter, M.C.: Maternal effects generate variation in life history: consequences of egg weight plasticity in the gypsy moth. Funct. Ecol. **5**(3), 386–393 (1991)
33. Sinervo, B.: The evolution of maternal investments in lizards: an experimental and comparative analysis of egg size and its effects on offspring performance. Evolution **44**, 279–294 (1990)
34. Sousa, T., Domingos, T., Kooijman, S.A.L.M.: From empirical patterns to theory: a formal metabolic theory of life. Phil. Trans. R. Soc. B (2007) (to appear)
35. Warham, J.: The crested penguins. In: Stonehouse, B. (ed.) The Biology of Penguins, pp. 189–269. MacMillan, London (1975)
36. Yoshinaga, T., Hagiwara, A., Tsukamoto, K.: Effect of periodical starvation on the survival of offspring in the rotifer Brachionus plicatilis. Fish. Sci. **67**, 373–374 (2001)
37. Zonneveld, C.: Animal energy budgets: a dynamic approach. Ph.D. thesis, Vrije Universiteit (1992)
38. Zonneveld, C., Kooijman, S.A.L.M.: Comparative kinetics of embryo development. Bull. Math. Biol. **3**, 609–635 (1993)